

GROUP MOTOR RESPONSES OF ADULT AND
LARVAL FORMS OF INSECTS TO DIF-
FERENT WAVE-LENGTHS
OF LIGHT

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This, the fifth paper of a series, relating to the group behavior of insects to colors, is concerned with the responses of seven species of Coleoptera and of sixteen species of lepidopterous, hymenopterous and coleopterous larvæ to ten wave-length bands of light of equal physical intensities, in disarray, from 3650 Å to 7400 Å. The tests were run in the sector type equipment described in the third and fourth papers of the series.¹ As outlined in these papers, the insects were placed in an introduction chamber, six feet away from the filter chambers, after the lamps were on and after all filter chambers were open. After the exposure period, the filter chambers, the central compartment, introduction chamber and dark chamber were closed, and counts were then made.

In all previous tests reported upon in the third and fourth papers the color filters were arranged in a sequence beginning with the shorter wave-lengths and extending successively to the longer wave-lengths, as follows: 3650 Å (ultra-violet); 4360 Å (violet-blue); 4640 Å (blue); 4920 Å (blue-blue-green); 5150 Å (blue-green); 5460 Å (yellow-green); 5750 Å (yellow-yellow-green); 6060 Å (yellow-orange); 6420 Å (orange-red); and 7200 Å (infra-red). Each filter chamber was separated from its neighbor by a black chamber.

All tests reported in the present paper, with adults and larvæ, were made with the filters in disarray, as follows: 3650 Å (ultra-violet); 6060 Å (yellow-orange); 4640 Å (blue); 7200 Å (infra-red); 5150 Å (blue-green); 6420 Å (orange-red); 5750 Å (yellow-yellow-green); 4360 Å (violet-blue); 5460 Å (yellow-green); and 4920 Å (blue-blue-green). The wave-length figures represent the peak transmissions of the filters.

¹ JOUR. N. Y. ENT. SOC., 50(1): 1-35, 1942; 51(2): 117-131, 1943.

Owing to the deterioration that occurred in the lamps used in previous tests, new forty-watt, frosted, Westinghouse Mazda lamps and a new General Electric Mazda mercury lamp (type A-H4, 100 watts) were utilized for all tests. The same method, outlined in our first paper,² was used for determining the relative positions of the lamps and various filter combinations so that the physical intensities were approximately equal. A slight change in technique, designed to improve the equalization, was recently made and this resulted in a new set of distance settings, differing slightly from those given in the first paper. These new distance settings are shown on page 29.

RESULTS WITH ADULT INSECTS

Table I presents the results of exposing seven species of Coleoptera to ten wave-length bands of light of equal physical intensities, in disarray, in the sector type equipment. By consulting the percentage distribution of those reacting positively to the various wave-length bands and by an examination of the group behavior curves in Figures 1 and 2, it may be noted that the peak response for all species except *Popillia japonica* took place in the ultra-violet (3650–3663 Å) and that secondary peaks occurred either in the blue-blue-green (4920 Å) or in the blue-green (5150 Å). Smaller numbers, in general, appear to have gone to 4360 Å (violet-blue) and larger numbers to 6060 Å (yellow-orange) than in previous tests when the filters were not in disarray. Except for the somewhat reduced attractiveness of 4360 Å and the slightly increased attractiveness of 6060 Å, the behavior patterns, with the filters in disarray, did not differ materially from previous patterns obtained with the filters in orderly array.

Peterson and Haeussler³ in their work with the Oriental fruit moth and colored lights found that when a less attractive colored light was placed at right angles to a more attractive colored one, more fruit moths went to the less attractive light than when the less attractive one was opposite the more attractive one. There is no doubt that the stimulating power of certain wave-lengths is influenced by their positions with respect to other wave-lengths. But the fact remains that except for the slight differences noted

² JOUR. N. Y. ENT. SOC., 49(1): 1–20, 1941.

³ Ann. Ent. Soc. Amer., 21(3): 353–379, 1928.

DISTANCE SETTINGS FROM 40-WATT LAMPS TO FILTER COMBINATIONS TO OBTAIN EQUAL LIGHT INTENSITY
(115-116 volts)

Filter combinations	Centimeters from lamp tip to filter for various percentages of transmitted light									
	100%	90%	80%	70%	60%	50%	40%	30%	20%	10%
244-397-555	22.6	24.3	26.1	28.3	30.8	34.8	39.8	47.0	59.6	cm.
243-978½	11.3	12.1	13.3	15.0	17.1	19.8	23.1	27.7	35.6	53.4
245-978	8.3	9.1	10.1	11.1	12.5	14.5	17.5	21.7	28.2	42.8
348-430	2.2	2.8	3.4	4.2	5.2	6.5	8.3	10.6	14.4	24.4
350-430-512	6.2	7.0	7.9	9.0	10.2	11.7	13.9	17.8	23.8	36.4
352-430-502	7.2	8.0	8.9	10.0	11.0	12.7	15.4	19.5	25.7	39.2
338-554	1.6	2.1	2.6	3.4	4.3	5.6	7.3	9.5	12.8	22.4
368-511½	1.2	1.6	2.2	2.8	3.6	4.8	6.4	8.7	11.7	20.8
038-611	0.9	1.3	1.8	2.4	3.2	4.3	5.9	8.0	11.1	19.6
Mercury lamp										
738-586	52.0	58.0	62.5	68.0	78.0	86.0	98.0	114.0

above the group behavior patterns for the species tested remained materially unchanged with the filters in disarray. Regardless of the relative positions of the various wave-length bands, the insects made approximately the same selections time after time.

RESULTS WITH LARVAL FORMS

Most of the experimental work on the behavior of insects to colored light has been done with adult insects. Nevertheless there are a few references in the literature to the behavior of larval forms and mention will be made of the photopositive ones.

For example, Mayer and Soule found that the larvæ of *Danaïa archippus* are photopositive to ultra-violet. Gross,⁴ in his study of the reactions of arthropods to monochromatic lights of equal intensities reported that the larvæ of *Zeuzera pyrina*, a lepidopterous wood-borer, and of a noctuid moth *Feltia subgothica*, are photopositive to colors, the order of the effectiveness of stimulation being blue (4200–4800 Å), green (4900–5500 Å), yellow (5700–622 Å), and red (6300–6500 Å). *Lymantria* larvæ, according to Hundertmark⁵ appear to prefer blue when different colors are compared. Götz,⁶ in his study of the perception of color and form in lepidopterous larvæ found that an appreciation of color occurs in the larvæ of *Vanessa* and *Pieris*. These are attracted by the green color of leaves or pieces of paper, regardless of the color of the surroundings, but more so on a white background than on a black one. Lammert⁷ reports that caterpillars will go toward a source of light after a blacking of their eyes. And Suffert⁸ states that many caterpillars colored like their surroundings and feeding in exposed situations, orient themselves so that the light always falls upon them from a particular angle. These last two instances indicate the possession of a dermal light sense.

Our tests as reported in the present paper involved the exposure of the larvæ of sixteen species of insects to ten wave-length bands of light, of equal physical intensities, from 3600 Å to 7200 Å. These bands were in disarray. From Table II and Figures

⁴ Jour. Exp. Zool., 14: 467–512, 1913.

⁵ Z. vergl. Physiol., 24: 563–582, 1936.

⁶ Z. vergl. Physiol., 23: 429–503, 1936.

⁷ Z. vergl. Physiol., 3: 225–278, 1925.

⁸ Z. Morph. Oekol. Tiere., 26: 147–316, 1932.

3, 4 and 5 which record their group behavior in percentages and graphically, it is apparent that the peak response for most species took place in the ultra-violet (3650 Å). In nearly all instances a peak either equal to the one in ultra-violet or secondary to it occurred in the blue-blue-green (4900 Å), or in the blue-green (5150 Å). The minor peak at 6060 Å (yellow-orange) is attributed to the disarray of the filters which resulted in this wavelength being next to 3650 Å (ultra-violet).

The larvæ of *Diacrisia virginica* were the only ones which ultra-violet light (3650 Å) failed to stimulate appreciably. These larvæ are found crawling upon the ground or feeding upon low plants. As a whole the group behavior of the larvæ, in general, did not differ from that of numerous adult insects, previously tested, and their color discrimination, so called, was approximately the same as that exhibited by adult insects in spite of the fact that their visual organs are less complex than those of adult insects.

NOTES

Autoserica castanea. This beetle, being nocturnal, was tested at 10:30 P.M.

Hippodamia convergens Guer. The predaceous larvæ of this coccinellid failed to react at all under the conditions of our tests. When placed in the introduction chamber they climbed up the sides and remained there. Apparently their negative geotropic behavior predominated.

Hyphantria cunea Dru. The $\frac{1}{2}$ to $\frac{3}{4}$ grown larvæ of this species, the fall webworm, made a web in the introduction chamber and stayed there, even though they had been previously deprived of food for twenty hours.

During the course of our work with larvæ it was found that, as a rule, they were more photopositive after having been deprived of food for a half-day or more previous to the tests. The gregariousness of some of the species, especially of the larvæ of *Hadena turbulenta* Hbn., and *Melalopha inclusa* Hbn., appeared to inhibit somewhat their sensitivity to light.

DISCUSSION

In view of the comparative simplicity of the lateral ocelli of larvæ, the similarity of the group behavior of larvæ to that of

adult insects with compound eyes is of considerable interest. Although variable in structure, lateral ocelli in lepidopterous larvæ consist of a group, each ocellus having a structure not unlike the single ommatidium of a compound eye. In the larvæ of sawflies and of many Coleoptera, the ocellus, of which there is only one on each side, is a lens-like, transparent thickening of the cuticle with underlying epidermis, and retinulæ, each made up of two or three visual cells grouped around a rhabdom. These visual cells may be pigmented, or there may be separate pigment cells. Dethier in a recent study⁹ of the corneal lens in caterpillars states that "the cornea possesses a short focal distance, great depth of focus, and an extremely low f value permitting the admittance of much light."

Although the king-crab, *Limulus polyphemus*, is not an insect, the work of Hartline and Graham on the nerve impulses and responses of single visual sense cells, to light, in the eye of this animal is of unusual interest and it is within the realm of possibility that a similar process of photoreception may operate in insects.

The lateral faceted eye of the king-crab contains about 300 large ommatidia and the optic nerve fibres come directly from the receptor cells with no intervening neurones. These authors¹⁰ studied the nerve impulses and developed a technique by which was recorded the discharge from a single receptor unit, in the form of oscillograms, representing the potential changes between the cut end and an uninjured portion of the nerve, upon stimulation of the eye by light. The electrical activity in the optic nerve brought about by this stimulation was amplified by a vacuum tube and recorded by an oscillograph. Among other things the stimulation of a single ommatidium resulted in a small strand of the optic nerve showing a regular sequence of nerve impulses. "The discharge in a single fiber begins after a short latent period at a high frequency, which has been found to be as high as 130 per second. The frequency falls rapidly at first, and finally approaches a steady value, which is maintained for the duration of illumination" (Hartline and Graham).

⁹ Jour. Cell. and Comp. Physiol., 19(3): 301-313, 1942.

¹⁰ Jour. Cell. and Comp. Physiol., 1(2): 277-295, 1932.

In a later paper¹¹ these authors studied the responses of single visual sense cells to visible light of different wave-lengths. This was done by means of single fiber preparations from a *Limulus* eye. It was found that when the energy of the stimulating light of different wave-lengths was approximately equal, the response to green was stronger than the responses to either violet or red. When the energy was increased in the red and violet their level of response was raised and when the intensities for the different wave-lengths were adjusted so that the responses were equal, there was no effect of wave-length as such, indicating that single sense cells can gauge brightness but cannot distinguish wave-length. The relative energies of the various wave-lengths required to produce the same response after being adjusted in inverse ratio to the degree to which they are absorbed yielded a visibility curve, for a single visual sense cell, that had its maximum in the green near 5200 Å and that declined symmetrically on each side to low values in the violet near 4400 Å and in the red near 6400 Å. According to the interpretation of visibility curves by Hecht and Williams¹² the stimulation of a single visual sense cell by light depends upon the absorption spectrum of the primary photosensitive substance. The absorption of light by this substance varies with wave-length and the production of a given response needs a certain amount of photochemical change, which in turn requires the absorption of a constant amount of energy.

Hartline and Graham also found that in the same eye of *Limulus* there was a differential sensitivity among optic nerve fibers and their attached sensory cells for different regions of the visible spectrum and they believe that such specialization of the visual cells, coupled with integrated action may give rise to color vision.

In considering the tests with insects reported upon in this and in previous papers,¹³ the following patterns of behavior prevailed over and over, when various species were exposed to ten wave-length bands of equal intensities from 3600 Å to 7200 Å. In the composite behavior¹⁴ of 5,454 insects of various orders, mostly

¹¹ Jour. Gen. Physiol., 18(6): 917-931, 1935.

¹² Jour. Gen. Physiol., 5: 1, 1922.

¹³ JOUR. N. Y. ENT. SOC., 49: 1-20, 149-159, 1941; 50: 1-35, 1942; 51: 117-131, 1943.

¹⁴ Ent. News, 54: 152-156, 1943.

coleopterous, the peak response took place at 3650 Å (ultra-violet). From here the response declined gradually to a low point at 4640 Å (blue); then it increased to a secondary peak at 4920 Å (blue-blue-green), and then declined gradually to a low point at 5750 Å (yellow-yellow-green) from which point it levelled off to 6420 Å (orange-red). In the cases of individual species there were deviations from this pattern. *Drosophila* and various species of Coleoptera in some tests responded almost entirely to 3650 Å alone, dropping to a low level at 4360 Å and levelling off at that wave-length. Sometimes the secondary peak occurred at 5150 Å instead of at 4920 Å. Although the peak responses took place at 3650 Å and 4920 Å, small percentages of the test animals went to other wave-lengths. In addition, it was found that when a second test, using the same insects, succeeded the first, the same group behavior pattern took place. The peak response occurred at 3650 Å, the secondary one at 4920 Å. However, the individuals that made up the peaks in the second test were not all the same as those making up the peaks in the first test. In other words, there was a shifting of the individuals that went to the different wave-length bands, but no difference in the final result.

Assuming that the light receptors of insects function in the same way as those of some other invertebrates and considering the results obtained from the single visual sense cells of *Limulus* as outlined by Hartline and Graham and mentioned above, it is possible to venture an explanation for the group behavior pattern of insect response to colors. Starting with the fact that the test insects responded in varying numbers to all wave-lengths from 3650 Å to about 6420 Å, it is apparent that the photosensitive substance of their visual sense cells will function at any of the wave-lengths between 3650 Å and 6420 Å, if the physical intensity of the wave-length is sufficient and constant.

When confronted by ten wave-length bands of equalized intensities which converged upon the insects in the introduction chamber of the apparatus, the primary photosensitive substance of the visual sense cells of a large number absorbed the energy at 3650 Å to a greater extent than the energy at other wave-lengths. This resulted in a photochemical reaction accompanied by physical

changes in nerve fibers, one of which was a change in the electric potential of the point in the fiber that was actively responding measured with respect to a nearby, but as yet, inactive point. This electrical activity in the optic nerve fiber was transmitted to the muscles where changes in tension occurred resulting in the insects going to the ultra-violet (3650 Å) in larger numbers than to any other test wave-length. As the absorption of light by the primary photosensitive substance of the single sense cell varies with wave-length and as the production of a response requires a certain amount of photochemical change plus a constant amount of energy, it seems evident that the energy of the remaining test wave-lengths although equal, was not sufficient to result in a response that equalled that of the ultra-violet. Consequently smaller numbers of individuals responded to the test wave-lengths other than 3650 Å. The question then arises as to why all individuals did not respond to 3650 Å alone. In a group of 100 or more insects collected in the field, it is not expected that they would all be in the same physiological state at the same time. In fact, when tested, only some are photosensitive. Others remain in the introduction chamber, others get as far as the central compartment and others go to the black chamber, all exhibiting different degrees of behavior to light. Among those that are photosensitive it is reasonable to assume that there exist some variations by individuals in the sensitivity of their visual receptors. These variations may be connected with different physiological states. They may be due to a depletion of the primary photosensitive substance in the visual sense cells through the action of light, resulting in individuals so affected responding in smaller numbers to wave-lengths other than ultra-violet. Until restorative processes take place in the visual sense cells of such individuals, their sensitivity to ultra-violet declines.

Frequently various species, when tested, responded almost exclusively to ultra-violet. But many others did not. In the case of *Drosophila* which was bred under controlled conditions and which were of uniform ages, the response to ultra-violet was unusually high.

It is realized that these deductions are based upon the behavior of single visual sense cells of the king-crab, to light of different

wave-lengths and no consideration has been given to the fact that individual cellular units act collectively and not independently, nor to the fact that Graham and Hartline¹⁵ found that although the visibility curves for single sense cells in the same eye are approximately identical, they differ by significant amounts. In addition they report that two sense cells were able to distinguish violet from red and taking all these facts into consideration they are of the opinion that such differential sensitivity "may be considered a peripheral mechanism of color vision."

Another reason for the deductions as outlined consists of the behavior of the Japanese beetle, *Popillia japonica*, which was made to respond to what were unattractive wave-lengths under equalized physical intensities, by increasing the intensities of such wave-lengths. In fact with other species as well it was possible to vary the behavior pattern by changing the intensities. And in general, from our work over the past several years, it appears that the behavior patterns of insects to equalized wave-lengths are not unlike the behavior pattern of a single sense cell, in *Limulus*, to equalized wave-lengths. Perhaps the behavior curves in this and in former papers¹⁶ may be interpreted as rough approximations of the absorption spectrum of the photosensitive substance in the combined visual sense cells of many insects, as well as indications of their motor responses to equalized wave-lengths of light.

A word should be said about the comparatively large percentages of test insects which remain in the introduction chamber and central compartment of our testing equipment. We have always attributed this mainly to low illumination. At low illuminations only the most sensitive ommatidia function, there being different thresholds of response for different ommatidia.¹⁷ By others, a falling off in intensity discrimination, due to low illumination is attributed to a nervous coupling of groups of ommatidia to form new units.¹⁸

¹⁵ Jour. Gen. Physiol., 18: 917-931, 1935.

¹⁶ Jour. N. Y. Ent. Soc., 49: 1-20, 149-159, 1941; 50: 1-35, 1942; 51: 117-131, 1943.

¹⁷ Hecht and Wald. Jour. Gen. Physiol., 17: 517-547, 1934.

¹⁸ Buddenbrock and Shultz. Zool. Jahrb. Physiol., 52: 513-536, 1933.

The foregoing discussion is an attempt to explain the group behavior patterns, or motor responses of insects to various wave-lengths of light of equal physical intensities on the basis of the results obtained by investigators who used single visual sense cells of other invertebrates. It is realized that the motor response to light of a complex organism such as an insect cannot be adequately and definitely explained on the basis of the behavior of single visual sense cells of other animals, nevertheless such work as has been done with single sense cells furnishes valuable clues to the phenomena of vision in insects. Until similar and additional investigations are made on the behavior of photoreceptor cells and optic nerve fibers of insects, singly and in integrated action, one has to be satisfied with implications.

PLATE V

Figure 1. Behavior of six lots of *Leptinotarsa decemlineata* Say, to 10 wave-length bands, in disarray, from 3650 Å to 7200 Å. Physical intensities equalized.

1. 129 beetles. Three tests.
2. 478 beetles. Four tests.
3. 857 beetles. Six tests.
4. 857 beetles. Four tests.
5. 340 beetles. Four tests.
6. 338 beetles. Four tests.

Figure 2. Behavior of six species of Coleoptera to 10 wave-length bands, in disarray, from 3650Å to 7200 Å. Physical intensities equalized.

1. *Chrysochus auratus* Say. 217 adults. Three tests.
2. *Tetraopes tetraophthalmus* Forst. 144 adults. Five tests.
3. *Chauliognathus marginatus* Fabr. 42 adults. Two tests.
4. *Photinus pennsylvanica* DeG. 78 adults. Three tests.
5. *Popillia japonica* Newm. 295 adults. Three tests.
6. *Autoserica castanea* Arrow. 338 adults. Three tests.

Tested after 10:30 P.M.

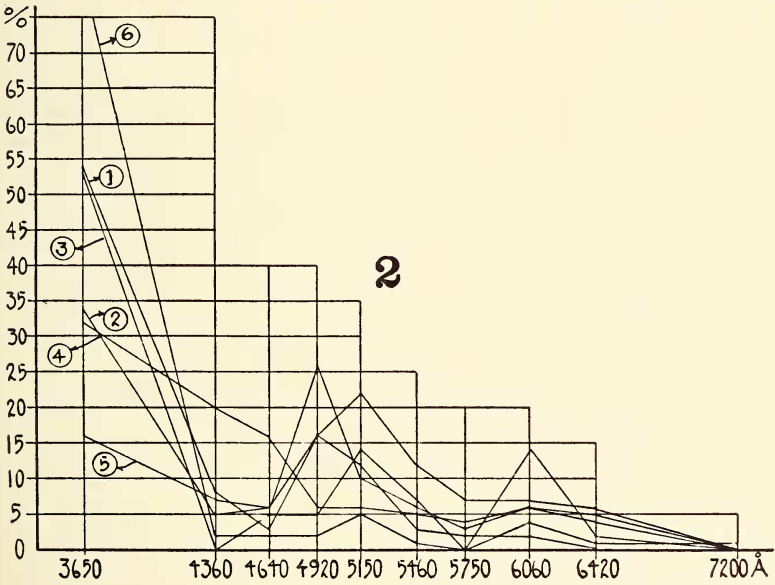
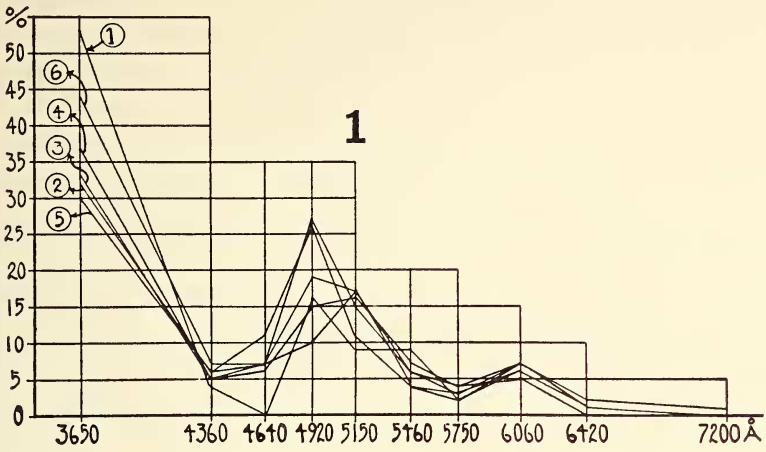


PLATE VI

Figure 3. Behavior of coleopterous, hymenopterous and lepidopterous larvæ to 10 wave-length bands, in disarray, from 3650 Å to 7200 Å. Physical intensities equalized.

1. *Leptinotarsa decemlineata* Say (Col.). 372 larvæ, $\frac{1}{2}$ to $\frac{3}{4}$ grown. Four tests.
2. *Lophyrus lecontei* Fitch (Hymen.). 124 larvæ, full grown. Two tests.
3. *Macremphytus* sp. (Hymen.). 491 larvæ, full grown. Three tests. Larvæ starved.
4. *Diacrisia virginica* Fab. (Lep.). 92 larvæ, full grown. Three tests.
5. *Dryocampa rubicunda* Fab. (Lep.). 100 larvæ, full grown. Three tests.
6. *Anisota senatoria* A & S (Lep.). 125 larvæ, $\frac{1}{2}$ to $\frac{3}{4}$ grown. Three tests.

Figure 4. Behavior of lepidopterous larvæ to 10 wave-length bands, in disarray, from 3650 Å to 7200 Å. Physical intensities equalized.

1. *Eudamus tityrus* Fab. 125 larvæ, full grown, starved. Three tests.
2. *Hadena turbulenta* Hbn. 263 larvæ, $\frac{3}{4}$ grown. Three tests.
3. *Datana integerrima* G. & R. 188 larvæ, $\frac{3}{4}$ grown, starved. Two tests.
4. *Datana ministra* Dru. 303 larvæ, $\frac{3}{4}$ to full grown. Three tests.
5. *Melalopha inclusa* Hbn. 70 larvæ, full grown. Two tests.
6. *Hyarpax aurora* S. & A. 274 larvæ, full grown. Three tests.

Figure 5. Behavior of lepidopterous larvæ to 10 wave-length bands, in disarray, from 3650 Å to 7200 Å. Physical intensities equalized.

1. *Actias luna* Linn. 63 larvæ, $\frac{3}{4}$ grown. Two tests.
2. *Telea polyphemus* Cram. 141 larvae, $\frac{3}{4}$ -full grown. Two tests.
3. *Telea polyphemus* Cram. 136 larvæ, full grown, starved. Four tests.
4. *Ceratonia catalpæ* Bdv. 110 larvæ, full grown. Three tests.
5. *Phlegethontius carolina* Linn. 32 larvæ, full grown. Two tests.

